

NEOTROPICAL MIGRATORY BREEDING BIRD COMMUNITIES IN RIPARIAN FORESTS OF DIFFERENT WIDTHS ALONG THE ALTAMAHA RIVER, GEORGIA

MALCOLM F. HODGES, JR.¹ AND DAVID G. KREMENTZ²

ABSTRACT.—We surveyed riparian forest corridors of different widths along the lower Altamaha River in Georgia in 1993 and 1994 to investigate the relationship between forest corridor width and Neotropical breeding bird community diversity and abundance. Species richness and abundance of three of six focal species increased with increasing forest corridor width. We suggest if Neotropical breeding bird communities are a target group, that land managers should consider leaving a 100 m buffer strip along riparian zones. *Received 28 Aug. 1995, accepted 13 Feb. 1996.*

Studies of the effects of forest fragmentation (Whitcomb et al. 1981, Lynch and Whigham 1984, Robbins et al. 1989) on communities of breeding birds in discrete forest blocks of different sizes have suggested that many Neotropical migratory bird species are sensitive to a reduction in forest area. More difficult to assess is the effect of reduction in width of riverine forest corridors on bird populations; although forest area may be reduced by encroachment from the corridor edge, these forests often remain contiguous with wider sections of the corridor. Stauffer and Best (1980) found that bird species richness increased from about 10–30 species with increasing width in wooded riparian habitats ranging from 10–200 m wide in Iowa. They noted, however, that seven of 17 species previously thought to be area sensitive bred in buffers ≤ 20 m wide. In a study of breeding birds in wooded riparian zones in Maryland and Delaware, Keller et al. (1993) found that Neotropical migrants were more area sensitive than were either short distance migrants or residents. Neotropical migrants increased in richness as corridor width increased, particularly in corridors < 200 m, while richness of the other bird groups remained relatively stable. Darveau et al. (1995) examined bird densities in riparian boreal forest corridors of different widths (20–300 m) which were bordered by recent (< 2 yrs old) clearcuts. They found that forest-breeding birds were sensitive to corridor width and concluded that 60-m wide corridors were required to maintain forest breeding birds. In all of these studies, the riparian zones were usually bordered by agricultural or clearcut fields. Studies in which the riparian zone is bordered by pine

¹ The Nature Conservancy of Georgia, 1401 Peachtree St. NW, Suite 236, Atlanta, Georgia 30309.

² National Biological Service, Patuxent Wildlife Research Center, Warnell School of Forest Resources, Univ. of Georgia, Athens, Georgia 30602-2152.

silviculture are apparently lacking. The adjacent habitat could conceivably ameliorate the species-area effect because the pine plantation might support some birds that would otherwise be absent in an agricultural or clear-cut landscape.

In the southeastern United States, forested wetlands are being lost or converted to pine silviculture at an alarming rate (Winger 1986, Hefner et al. 1994). However, at present, land managers have no information about how wide a buffer strip adjacent to streams is necessary to maintain functional breeding bird communities. Understanding bird-habitat relationships is important both locally and over broad areas because forest health may depend on the presence of breeding birds. Forest-dwelling birds have been shown to control the numbers of insects feeding on tree foliage (Marquis and Whelan 1994). Further, recreation dollars associated with more natural forests are becoming a consideration in forest management (Wiedner and Kerlinger 1990, Kerlinger 1993).

We investigated the relationship between width of bottomland hardwood forest corridors along the Altamaha River in Georgia and breeding populations of Neotropical migratory birds. Our objectives were to examine the relationship between forest corridor width and bird species richness, density, and the probability of encountering a particular bird species.

STUDY AREA AND METHODS

We studied birds on the Altamaha River floodplain swamp, which begins at the confluence of the Ocmulgee and Oconee rivers at river km 212 in Montgomery and Jeff Davis counties, Georgia. These forests extend downstream to the Buffalo and Clayhole swamps at approximately river km 24 in Glynn and McIntosh counties. The three dominant community types sampled were: willow oak (*Quercus phellos*), overcup oak (*Q. lyrata*)-water hickory (*Carya aquatica*), and bald cypress (*Taxodium distichum*)-water tupelo (*Nyssa aquatica*) (Allard 1990). The first was a wet-mesic river floodplain forest dominated either by willow oak or laurel oak (*Q. laurifolia*), with several other hardwoods and bald cypress occurring in the canopy. The second was a wet river floodplain forest dominated in the canopy by overcup oak and water hickory. The third, a forested riverine swamp, was dominated by bald cypress and either water tupelo or Ogeechee lime (*N. ogeche*) in the canopy and was flooded for most of the year. Some small stream corridors were sampled which were swamp forests with the same floristic components as riverine bottomlands but with narrower zonation and less frequent flooding.

Variable length transects were placed perpendicular to the river, based on corridor width, shape, lack of disturbance, and presence of adjacent pine plantations. Riverine forest corridors were rejected if they had been extensively thinned or were in an early successional stage (trees <8 cm dbh), excessively convoluted at the pine plantation edge, within 100 m of other large forest tracts, or in close proximity to a major highway. Transects were located ≥ 500 m apart. Three corridor-width classes were used: narrow (<350 m), medium (400–700 m), and wide (>1000 m). Generally the Altamaha River meandered within a fairly defined (about 1500 m wide) bottomland which was bordered by pine plantations. Thus,

TABLE 1

NEOTROPICAL MIGRATORY BREEDING BIRDS KNOWN TO BREED IN SOUTH ATLANTIC COASTAL
PLAIN FORESTS (ADAPTED FROM GAUTHREAUX 1992)^a

Common Name (Scientific Name)

American Swallow-tailed Kite*	(<i>Elanoides forficatus</i>)
Mississippi Kite	(<i>Ictinia mississippiensis</i>)
Broad-winged Hawk	(<i>Buteo platypterus</i>)
Yellow-billed Cuckoo	(<i>Coccyzus americanus</i>)
Ruby-throated Hummingbird	(<i>Archilochus colubris</i>)
Eastern Wood-Pewee*	(<i>Contopus virens</i>)
Acadian Flycatcher	(<i>Empidonax virescens</i>)
Great Crested Flycatcher	(<i>Myiarchus crinitus</i>)
Blue-gray Gnatcatcher	(<i>Poliophtila caerulea</i>)
Wood Thrush	(<i>Hylocichla mustelina</i>)
White-eyed Vireo	(<i>Vireo griseus</i>)
Yellow-throated Vireo	(<i>V. flavifrons</i>)
Red-eyed Vireo	(<i>V. olivaceus</i>)
Northern Parula	(<i>Parula americana</i>)
Yellow-throated Warbler	(<i>Dendroica dominica</i>)
Prothonotary Warbler	(<i>Protonotaria citrea</i>)
Swainson's Warbler	(<i>Limnithlypis swainsonii</i>)
Louisiana Waterthrush	(<i>Seiurus motacilla</i>)
Kentucky Warbler	(<i>Oporornis formosus</i>)
Hooded Warbler	(<i>Wilsonia citrina</i>)
Summer Tanager	(<i>Piranga rubra</i>)

^aThose species marked with an asterisk (*) were not recorded in sampling for the present study, although they were noted during other field work in the Altamaha River basin in 1993 or 1994.

when a wide corridor transect was chosen, the corridor width on the other side of the river tended to be narrow and vice versa. The Altamaha River, which usually exceeded 100 m in width, seemed to act as an effective barrier against cross stream movement of five of our focal species (MFH, unpubl. data). The only exception was the Prothonotary Warbler (scientific names in Table 1) which was observed frequently flying across the river. We selected 10 transect sites in 1993: four narrow (36–135 m), three medium (480–660 m), and three wide (1320–2088 m). From one to seven points were located along these transects for a total of 31 points. Points were located 50 m from the pine plantation edge and at 200 m intervals thereafter. Most transects were located in forested riverine swamps and wet and wet-mesic river floodplain forests. Exceptions included three narrow transects in which relatively steep (>30% slope) mesic bluff forests were part of the forest corridor.

In 1994, we sampled six of the 10 transects used in 1993, and 16 additional transects were added. Two medium and two wide transects sampled in 1993 were deleted because of marginal habitat characteristics. New transects added in 1994 included 14 narrow transects located in small stream corridors closely associated with the Altamaha River, one medium transect, and one wide transect. Totals for 1994 were 18 narrow (36–330 m), two medium (440–510 m), and two wide (1320–1512 m) transects, with 38 points surveyed.

We used the variable circular plot technique (Reynolds et al. 1980) to sample birds at points along each transect. In 1993, each point was sampled three times during 16–31 May,

1–15 June and 16–30 June. Sampling was confined to the first two periods in 1994. MFH was the only observer for all sampling. Order of sampling was stratified so that each point was sampled at least once within 1.5 h after sunrise. All sampling occurred within 4 h after sunrise.

All birds heard or seen during a 10-min sampling period were recorded, although only Neotropical migrants were used in these analyses (Table 1). We summed the number of species recorded at all points by corridor width to estimate species richness.

We recorded bird numbers at three distances: <25 m, 25–50 m, and >50 m. Each species had a maximum detectable range determined by calculating the ratio of birds per unit area within 50 m of the counting point to birds per unit area beyond 50 m and solving for the unknown area. The cut-off points for the species used in density estimates were Acadian Flycatcher—70 m, Blue-gray Gnatcatcher—50 m, White-eyed Vireo—80 m, Red-eyed Vireo—80 m, Northern Parula—80 m, and Prothonotary Warbler—100 m.

The structure of the plant community was sampled along each transect at five points at 10 m intervals on either side of each sampling point (10 points total for each sampling point). Percent canopy cover (>3 m height) and shrub cover (1–3 m height) were estimated using an ocular tube. The plant community type at each sampling point was deduced from plant species lists compiled at each sampling point (Allard 1990). We estimated the timber basal area at the sampling point with a cruising angle. Landsat TM and SPOT satellite imagery were used to measure the width of the forest corridor from river to pine plantation edge for each transect.

We estimated density per ha by corridor width and year for each species with sufficient data. Data consisted of the single count (3 in 1993, 2 in 1994) which had the highest number of birds detected. Densities of Neotropical migrants were estimated using the program DISTANCE (Laake et al. 1993). Three models (uniform, half-normal, hazard-rate) were evaluated using likelihood ratio tests to determine which model best fit the data. Once the final model was selected, we tested for annual differences in densities of each species within each corridor width by determining if the 95% confidence limits overlapped. We also tested for annual effects by fitting a nested logistic regression (PROC LOGISTIC, SAS 1990) model with corridor width and year effects versus corridor width only. The response variable was presence/absence of each species. Model selection was based on Akaike's information criterion (Akaike 1973).

Sensitivity to corridor width was examined using logistic regression (PROC LOGISTIC, SAS 1990). To produce a data set comparable to that of Keller et al. (1993) who sampled at the center of each riparian corridor, we subsampled those data taken from the approximate middle of each transect. At these points, a presence/absence data set was produced for each species. This response variable was then modelled, using corridor width as a predictor. Based on the parameter estimates, we calculated the estimated probability of a species occurring in a corridor of given width (PROC LOGISTIC, SAS 1990:1076).

Next, we examined whether species density was more closely related to the vegetative characteristics within the corridors or to corridor width alone. Because correlations were noted among vegetation measurements (unpubl. data), we reduced the three vegetation variables (percent canopy cover, percent shrub cover, timber basal area) into two variables (PC1, PC2) using principal components analysis (PROC PRINCOMP, SAS 1990). We then modelled the response variable, density of each species at a point, with the predictor variables corridor width, distance from the pine edge, PC1, and PC2 (PROC GLM, SAS 1990). To insure that birds were not responding to inherent differences in the vegetation among corridor widths, we examined the relationships among corridor width class and the predictor variables PC1 and PC2 by year and across years.

Finally, we examined the relationship between species richness and corridor width using

a generalized linear model (PROC GLM, SAS 1990) with year, corridor width, and year*corridor width as predictors.

RESULTS

We detected 48 bird species on the surveys, of which 19 were Neotropical migratory breeding birds (Table 1). Species richness ranged from four to 15 across all corridor widths with 4–14 in narrow, 11–13 in medium, and 12–15 in wide corridors. The third sampling period in 1993 did not add any unique species to measurement of species richness beyond those observed during the first two sampling periods. Species richness varied by corridor width and year ($F_{1,31} = 3.48$, $P = 0.07$), with narrow corridors having lower mean species richness (7.8 ± 2.48 SD) than either medium (12.0 ± 0.71) or wide (12.6 ± 1.52) corridors ($P < 0.05$). More species were recorded in 1993 than in 1994 ($F_{1,31} = 10.94$, $P = 0.002$).

Six species occurred in sufficient numbers to estimate their densities: Acadian Flycatcher, Blue-gray Gnatcatcher, White-eyed Vireo, Red-eyed Vireo, Northern Parula, and Prothonotary Warbler. The highest counts always occurred during the second survey, followed by the first survey, and finally the third survey. The third survey in 1993 added little to the results. There were no differences in densities of any species between years in either the medium or wide corridors ($P > 0.05$). Comparing all narrow corridors, densities of Acadian Flycatcher, Blue-gray Gnatcatcher, White-eyed Vireo, and Northern Parula in 1994 were lower than in 1993 ($P < 0.05$). Examining just those narrow transects surveyed in both years (versus examining all narrow transects surveyed in both years), no differences in densities were found between years ($P > 0.05$). Apparently, the new transects sampled in 1994 were responsible for the overall differences in densities between years for the narrow corridors. Thus, we believe that the differences between densities for the 1993 and 1994 narrow transects reflected habitat differences rather than annual differences. Those narrow transects added in 1994 were in small stream corridors closely associated with the Altamaha River, unlike the exclusively riverine corridors used in 1993. Logistic regression indicated that only the White-eyed Vireo demonstrated a difference ($P < 0.05$) in presence/absence between years, with fewer White-eyed Vireos being seen in 1994. Based on the combination of these two tests, we believe that there was no strong evidence for an effect of year on densities for these six species. Thus we combined data from both years in subsequent analyses.

For all six species, densities were higher in medium corridors than in either narrow or wide corridors (Table 2). However, the differences in

TABLE 2
 DENSITY ESTIMATES PER HECTARE AND 95% CONFIDENCE INTERVALS OF SIX FOCAL SPECIES
 OF NEOTROPICAL MIGRATORY BREEDING BIRDS BY CORRIDOR WIDTH (CW), ALTAMAHA
 RIVER BASIN, 1993 AND 1994^a

Species	CW ^b	Est. density	Confidence interval
Acadian Flycatcher	N	0.08	0.05–0.15
	M	0.10	0.08–0.12
	W	0.05	0.04–0.07
Blue-gray Gnatcatcher	N	0.07	0.04–0.15
	M	0.11	0.08–0.15
	W	0.08	0.04–0.17
White-eyed Vireo	N	0.06	0.04–0.10
	M	0.12	0.06–0.22*
	W	0.06	0.04–0.09
Red-eyed Vireo	N	0.08	0.04–0.14
	M	0.16	0.13–0.21
	W	0.06	0.05–0.07
Northern Parula	N	0.09	0.05–0.16
	M	0.22	0.16–0.31*
	W	0.07	0.06–0.08
Prothonotary Warbler	N	0.03	0.01–0.05
	M	0.07	0.04–0.13
	W	0.05	0.04–0.07

^a An asterisk (*) denotes that the density estimate is significantly ($P < 0.05$) different than either of the other density estimates for that species.

^b N = narrow corridors; M = medium corridors; W = wide corridors.

density were significant ($P < 0.05$) only for White-eyed Vireos and Northern Parulas.

Northern Parulas, White-eyed Vireos and Red-eyed Vireos exhibited significant relationships between corridor width and probability of occurrence ($P < 0.05$, Fig. 1). The response to increasing corridor width was most pronounced between 50 and 100 m. There was a greater than 80% chance of five of the six species, excluding Prothonotary Warbler, being detected in a 100 m wide corridor strip. Although not significantly so, both the Blue-gray Gnatcatcher and the Prothonotary Warbler were more likely to be found in wider corridors, whereas the Acadian Flycatcher was less likely to be found in wider corridors (Fig. 1).

PC1 and PC2 had eigenvalues >1 which is the usual cut-off point for inclusion in analyses such as ours (Nichols 1977). PC1 accounted for 36% of the variation in the three vegetation variables, while PC2 accounted for 32% for a cumulative accounting of 68% of the variation in vegetation variables. PC1 was positively associated with timber basal area and canopy cover and negatively associated with shrub cover. We

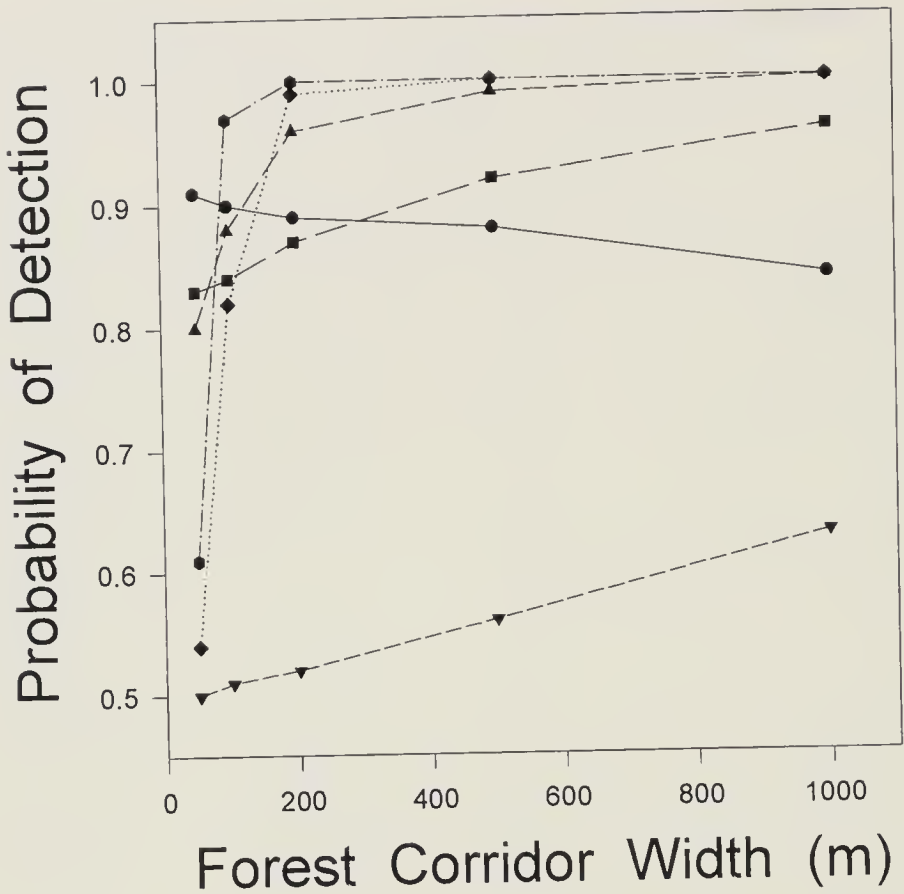


FIG. 1. Probability of detecting six focal species of migratory breeding birds along the Altamaha River riparian forest corridor. Solid circle—Acadian Flycatcher, square—Blue-gray Gnatcatcher, triangle (point up)—Northern Parula, triangle (point down)—Prothonotary Warbler, diamond—Red-eyed Vireo, hexagon—White-eyed Vireo. Points represent estimated probabilities of detection at 50, 100, 200, 500, and 1000 m corridor widths.

interpret this score, when high, as reflecting forest stands with a relatively closed canopy and little undergrowth. PC2 was positively associated with canopy cover and shrub cover reflecting forests with closed canopies and more undergrowth. Species-specific modelling revealed that Prothonotary Warbler and Red-eyed Vireo densities were positively related to PC1 ($P < 0.05$), while White-eyed Vireo density was negatively related to PC1 ($P < 0.05$). In addition, the density of Red-eyed Vireos was related positively to the distance from the pine-plantation edge ($P < 0.05$), while White-eyed Vireo abundance was positively related to corridor width ($P < 0.05$).

We found that vegetation structure differed by corridor width in 1993 ($F_{2,16} = 4.02$, $P = 0.04$) but not in 1994 ($F_{2,37} = 2.64$, $P = 0.09$). In 1993, the difference in vegetation structure was due to PC2, the amount of shrub cover. Combining years, there was no difference in vegetation structure ($F_{2,54} = 1.97$, $P = 0.15$).

DISCUSSION

The Neotropical migratory breeding bird community that we sampled along the Altamaha River was typical of what would be expected in the southeastern United States (Table 1; Hamel 1992). Only two species of Neotropical migrants were absent from our surveys, American Swallow-tailed Kite and the Eastern Wood-Pewee. The former probably has one of the lowest densities among breeding birds of Altamaha River bottomland forests, while the latter is not found in bottomland habitats in our area, preferring mature pine woodlands (MFH, pers. obs., Hamel 1992). Although the bird community that we monitored was typical, we point out that the Altamaha River and its associated riparian zone are not typical of the southeastern United States. The Altamaha River has the largest watershed in the Southeast (Anonymous 1986) and is famous for its extensive associated tracts of unbroken bottomland hardwoods (Wharton et al. 1982). Clearly these forested tracts are unusual today, and so our findings may not be entirely applicable to other riverine systems in the Southeast.

Species richness values by corridor width increased with area as Keller et al. (1993) found. The year effect we observed was, in part, a result of incorporating small stream corridors in 1994 which had, across the board, lower species richness values. Despite these differences in habitat types, all corridor widths had lower species richness in 1994; we are unsure why.

Of the six species for which we could estimate the probability of detection, five exhibited a trend towards increasing detection with increasing forest corridor width, three significantly so. Four of these species, Acadian Flycatcher, Prothonotary Warbler, White-eyed Vireo, and Red-eyed Vireo showed the strongest relationship between probability of detection and increasing forest corridor width (Keller et al. 1993). Keller et al.'s (1993) evidence for the Acadian Flycatcher was opposite from ours though, as we found Acadian Flycatchers tended to decrease in abundance with increasing corridor width (although not significantly). Robbins et al. (1989) and Dawson et al. (1993) both found the Acadian Flycatcher to be area sensitive (positively) in non-riparian forested situations in Maryland. The Prothonotary Warbler was area sensitive (positively) for Keller et al. (1993) but not for Robbins et al. (1989) or us.

The relationship observed between densities of the six species and corridor width was unexpected. We had anticipated that the highest densities would have occurred in the widest corridors, assuming that the widest corridors would have contained not only more total habitat but also habitat of higher quality. Our finding that vegetation structure was not consis-

tently related to corridor width indicated that wider corridors were not structurally different than narrower corridors. Despite the lack of differences in habitat structure that we measured, the differences in densities suggest either that differences in habitat quality existed, which we did not measure, or behavioral factors excluded some birds from the widest corridors. As Van Horne (1983) and Pulliam (1988) have asserted, high animal densities may result from excessive numbers of immigrants who have been forced away from the preferred habitat by higher ranking (more dominant) individuals. If true, then the lower densities in the widest corridors might reflect a predominance of more successful, more dominant individuals who benefit by controlling densities.

In the generalized linear model examining sensitivity to corridor width, vegetation parameters, and distance to pine edge, White-eyed Vireo was the only species whose numbers clearly showed a positive association with corridor width. During the breeding season, this species is not restricted to forest interiors; it frequently uses young second growth and other shrubby habitats. White-eyed Vireo's negative associations with canopy density and basal area and positive association with shrub density are easier to predict (Hamel 1992). Other studies (Robbins et al. 1989) have noted sensitivity to forest area for species common in our area, such as Acadian Flycatcher and Northern Parula. The much larger data set of Robbins et al. (1989) may have contributed to their better rate of detection of significant positive associations with forest area. Red-eyed Vireo numbers showed a positive association with distance from the pine-plantation edge, indicating a preference for forest interiors, and a preference for closed canopies, the latter having been noted previously (Robbins et al. 1989).

The rapid increase in probability of occurrence and species richness with increasing corridor width and the apparent asymptotic shape of the species abundance-area curves suggests that forest corridors of about 100 m should be sufficient to maintain functional assemblages of the six most common species of breeding neotropical migratory birds. This guideline exceeds the 60 m recommended by Darveau et al. (1995), but comparing boreal forests and southeastern bottomland hardwoods may not be appropriate. Our guideline does concur with the findings of Keller et al. (1993) who also recommended a 100 m wide corridor be maintained. Our recommendation does not take into account the needs of the least common species of Neotropical migratory birds encountered, which we were not able to ascertain from these data.

The value of corridors goes beyond the maintenance of breeding bird communities, as Naiman et al. (1993:209) concluded that "effective riparian management could ameliorate many ecological issues related to

land use and environmental quality." More specifically, Winger (1986) demonstrated that functional forested corridors assimilate nutrients and organic matter, hasten the degradation of persistent pesticides and decrease the bioavailability of heavy metals. Justification of streamside corridors thus goes beyond breeding bird communities alone (see also Brinson et al. 1981).

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